Fecundity and reproductive potential of Scotia-Fundy summer- and autumn-spawning herring (Clupea harengus L.)

G.J. Óskarsson*, C.T. Taggart and R.L. Stephenson**

Oceanography Department, Dalhousie University, 1355 Oxford Street, PO Box 15000, Halifax, NS, B3H 4R2, Canada

**St. Andrews Biological Station, 531 Brandy Cove Rd., St. Andrews, New Brunswick, E5B 2L9, Canada

*Present address: Marine & Freshwater Research Institute, Skulagata 4, 121 Reykjavik, Iceland
E-mail: gudmundur.j.oskarsson@hafogvatn.is

2016

Canadian Technical Report of
Fisheries and Aquatic Sciences 3182

Fisheries and Oceans Canada | Pêches et Océans Canada

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts.*

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

© Her Majesty the Queen in Right of Canada, 2016.

Cat. No. Fs 97-6/3182E-PDF ISBN 978-0-660-06591-5 ISSN 1488-5379

Correct citation for this publication:

Óskarsson, G.J, Taggart, C.T. and Stephenson, R.L. 2016. Fecundity and reproductive potential of Scotia-Fundy summer- and autumn-spawning herring (*Clupea harengus* L). Can. Tech. Rep. Fish. Aquat. Sci. 3182: 7 + 27 p.

TABLE OF CONTENTS

ABSTRACT V
RÉSUMÉ VI
1. INTRODUCTION 1
2. MATERIAL AND METHODS 2
2.1. FECUNDITY 2
2.2. TOTAL EGG PRODUCTION 2
2.2.1. Body condition and stock-specific biological variables 2
2.2.2. Estimation of E and SSB 3
2.2.3. Comparison with historical fecundity data 4
2.3. STATISTICAL METHODS 4
3. RESULTS 4
3.1. FECUNDITY 4
3.2. TOTAL EGG PRODUCTION 5
3.2.1. Body condition and stock specific biological variables 5
3.2.2. Estimation of E and SSB 6
3.2.3. Comparison with historical fecundity data 6
4. DISCUSSION 7
5. ACKNOWLEDGEMENTS 11
6. REFERENCES 11
7. TABLES 15
8. FIGURES 18

ABSTRACT

Fecundity and reproductive potential of Scotia-Fundy summer- and autumn-spawning herring (*Clupea harengus* L.): vii + 27 p.

Total egg production (E) by a fish stock, estimated using fecundity relationships, has been postulated to provide a superior estimate of a stock's reproductive potential relative to the spawning stock biomass (SSB) estimate. We examined variation in the fecundity of Scotia-Fundy Atlantic herring using ovaries from 100 fully mature individuals collected on German Bank, NW Scotian Shelf, in September 2001 and in relation to historical fecundity estimates. Potential fecundity (F_P; number of vitellogenic oocytes in mature ovaries) was a linear function of total length (r^2=0.89). Length-specific F_P was weakly (r^2=0.10) and positively related to Fulton's body condition index (K) and relative fecundity (eggs per unit somatic weight) was a positive linear function of total length (r^2=0.61). The length-specific fecundity estimates in 2001 were higher than estimates recorded during the late 1960s and mid 1970s and the difference is not adequately explained by K or other factors. Decreases in length-at-age, age- and length-at-maturity and total egg production, particularly contributions from the larger (older) spawners, were observed over the period 1970-2001 and are consistent with changes that could be induced through size-selective fishing practices that target larger (faster growing and late maturing) individuals. The relationship between annual estimates of E and SSB for the stock over the same period approached proportionality with both recruit and repeat spawners indicating that reproductive potential may be adequately estimated from SSB. Partitioning the reproductive potential between recruit and repeat spawners or among different age or length classes may prove to be essential when determining the recruitment potential of the stock.

RÉSUMÉ

Fécondité et potentiel reproducteur des fraies d'été et d'automne du hareng (*Clupea Harengus* L.) de Scotia-Fundy: vii + 27 p.

La production totale d'œufs (E) d'un stock de poisson, estimée en utilisant les relations de fécondité avec la taille, a souvent été suggérée comme étant une meilleure estimation du potentiel reproductif des stocks que l'estimation de la biomasse des stocks de géniteurs (BSG). Nous avons étudié la variation de la fécondité des harengs de l'Atlantique de la Nouvelle-Écosse/Baie de Fundy à partir de l'examen d'ovaires de 100 individus matures collectés sur le banc German localisé sur le plateau néo-écossais nord-ouest, en septembre 2001, et en les comparant avec les estimations de fécondité historiques. La fécondité potentielle (F_P; le nombre d'ovocytes vitellogènes dans des ovaires matures) était linéairement corrélée à la longueur totale du poisson (r^2=0.89). La F_P spécifique à la longueur était positivement corrélée avec le coefficient de Fulton (K) mais la corrélation était relativement faible (r^2=0.10). La fécondité relative (œufs par unité de poids somatique) elle, était fortement corrélée de façon linéaire à la longueur total du poisson (r^2=0.61). Les estimations de fécondité spécifique à la longueur pour l'année 2001 étaient plus élevées que celles faites à la fin des années 1960 et au milieu des années 1970. Cette différence n'est pas expliquée de manière cohérente par le coefficient de Fulton (K), ni par d'autres facteurs. En revanche, l'observation d'une diminution de la taille atteinte pour un certain âge, de l'âge et de la taille atteints à la maturité, et également de la production totale des œufs (particulièrement la contribution des plus grands géniteurs - les plus vieux), entre 1970 2001, était cohérante avec les changements induits par une pratique de pêche sélective, visant les individus larges qui grandissent vite et deviennent matures plus vieux. La relation entre les estimations annuelles de E et BSG pour le stock durant la même période approche une proportionnalité à la fois pour les recrues et les géniteurs ayant frayés plusieurs fois, ce qui indiquerait que le potentiel reproductif peut être estimé de manière adéquate à partir du BSG. Une partition du potentiel reproductif, entre les recrues et les géniteurs ayant frayés plusieurs fois, ou entre les différentes classes d'âges ou de longueurs, pourrait être essentielle pour évaluer le recrutement potentiel des stocks de poisson.

1. INTRODUCTION

Total egg production (E) is a first approximation of the reproduction potential of a fish stock and therefore of recruitment potential. While various models describing stock-recruitment (*SR*) relationships (e.g., Ricker 1954; Beverton and Holt 1957; Cushing 1988; Shepherd 1982; Mackinson et al. 1999) proportionately equate E with recruitment potential, spawning stock biomass (SSB) is the conventional and most frequently used proxy based on the assumption that E is proportional to SSB. The assumption of direct proportionality has been challenged (Rijnsdorp 1994; Marshall et al. 1998; Cardinale and Arrhenius 2000; Marshall 2009; Óskarsson and Taggart 2006; 2010). The challenges are based, in part, on observations that potential fecundity (F_P) is dependent on somatic body weight (W), where F_P is defined as the number of vitellogenic oocytes in the pre-spawning ovaries, and relative fecundity ($RF_P = F_P\ (W\text{-}OW)^{-1}$; where OW is ovary weight) is length-dependent. A logical hypothesis stemming from the above is that E varies with the size (length) composition of the stock and can therefore violate the assumption that E is proportional to SSB. A comprehensive literature search (see Óskarsson and Taggart 2006), revealed that stock specific F_P appears, without exception, to be dependent on fish size and (or) age. Often, annual residual variation, or residual variation among individuals, is observed around the length specific F_P relation that can be explained by variation in fish condition (Óskarsson and Taggart 2006; Damme et al. 2009; Rideout and Morgan 2010; Kennedy et al. 2011), weight-at-length (Óskarsson et al. 2002), stock abundance (Kelly and Stevenson 1985; Lambert 1987; Bailey and Almatar 1989), and density-independent factors (Stares et al. 2007). Although many studies have shown that body weight is a strong explanatory variable for fish fecundity (e.g., Rideout and Morgan 2010), the literature implies that annual variation in body condition and the length composition of a stock will affect estimates of E and thus E is not necessarily proportional to SSB. The violation of the proportionality assumption has implications for fishery management that generally relies on biological reference points determined from fishing mortality, recruitment, and SSB with an assumed proportionality to E.

The Scotia-Fundy summer- and autumn-spawning (SFS) Atlantic herring (*Clupea harengus*) stock complex in management unit 4WX on the Atlantic Coast of Canada (Power and Iles 2000) has three major spawning grounds (Stephenson et al. 2009; Fig. 1). There are typically several spawning waves at each spawning ground within a season (Lambert 1987; McPherson et al. 2001; 2003) and spawning can last for over two months from the end of July through September (Lambert 1987; Óskarsson 2005). Annual SSB estimates for the SFS herring stock, over the period 1970 through 2001, have fluctuated over a 5-fold range (170×10^3 tonnes to 820×10^3 tonnes) and total annual landings show a 3-fold range (60×10^3 and 200×10^3 tonnes) over the same period (Stephenson et al. 1993; Power et al. 2011).

Our main objective is to use SFS herring data to asses the validity of the commonly applied assumption of proportionality between E and SSB. We investigate variation in fecundity and total egg production for the SFS herring stock by examining variation in F_P and the factors that may affect E; e.g., variation in number of female spawners, their sizes, and associated body condition. In particular, we examine the relationship between E and SSB in estimating the reproductive potential of the stock and evaluate the proportionality assumption. We also assess changes in stock fecundity over the recent three decades by comparing the contemporary estimates of F_P with those provided in earlier studies (Perkins and Anthony 1969; Messieh 1976).

2. MATERIAL AND METHODS

2.1. FECUNDITY

Random samples of SFS herring were collected on German Bank, SW Nova Scotia (43° 30'N, 66° 19'W) on 19 September 2001 during the spawning season. One hundred ovaries from ripe, pre-spawning females, regardless of maturity stage (below), were then randomly selected to determine total length (L; ±0.1 cm), whole-body weight (W; ±0.1 g), and maturity stages 1–8 (1–2 immature, 3–5 maturing, 6 spawning, 7 recently spawned and 8 recovering; Bowers and Holliday 1961; Anon. 1962). The ovaries of each fish were then removed, weighed (OW; ±0.1 g) and preserved in 4.8% buffered formaldehyde solution. The wet-weight of the preserved ovaries (OW_P) was again recorded in the lab and three sub-samples (s representing number of subsamples) of 150 to 250 mg (±1 mg) were excised from each of 60 ovaries and weighed (OW_s). Two sub-samples were taken from the remaining 40 ovaries, and as the differences in F_P estimates between sample pairs were <5%, we considered the precision acceptable relative to the estimates provided by the other 60 ovaries (Óskarsson et al. 2002; Óskarsson and Taggart 2006). We counted the number of vitellogenic oocytes in each sub-sample (N_s) using a binocular microscope. Annual potential fecundity (F_P) was then calculated using the gravimetric method:

$$F_P = \sum_{i=1}^{s} \left(N_s \times OW_s^{-1} \right) \times OW_p \times s^{-1} \quad (1).$$

2.2. TOTAL EGG PRODUCTION

2.2.1. Body condition and stock-specific biological variables

The estimation of total egg production by the stock requires fecundity estimates (above), stock abundance estimates, and the associated estimates of the size and age composition of the spawners. Historical stock-sampling records (Fisheries and Oceans Canada (DFO), St. Andrews Biological Station) consist of L and W measures, maturity stage, and age (year) derived from otoliths, for 56×10^3 mature and 31×10^3 immature SFS female herring collected over the period 1970 through 2001 (Table 1). These data were used to provide annual (Y) estimates of the body condition anomaly, $K_{anom,Y}$, during the pre-spawning season (see Óskarsson and Taggart 2009), where $K=100W\,L^{-3}$ (g cm^{-3}). Average K ($\overline{K}_{I,L_c,m}$) was calculated over all years for individuals among two length classes (L_c; 28–31 cm and 32–35 cm, inclusive), two maturity classes respectively (m; stage-3 and -4 combined, and stage-5), and for consecutive 15-day-of-the-year intervals (I) from day-of-year 130–300 inclusive. Condition analyses were restricted to the above length classes because they were >98% mature over the 32-year period, they consisted primarily of repeat spawners, and the maturity stages and the sampling window ensured samples were representative of spawning herring.

The difference between average and individual condition estimates provided the residual:

$$KR_{Y,I,L_c,m} = K_{Y,I,L_c,m} - \overline{K}_{I,L_c,m} \quad (2).$$

The residuals averaged over each year, where n_Y represents the number of fish in year Y, provide the annual condition anomaly (K_{anom}):

$$K_{\text{anom},Y} = \sum_{i=1}^{n_Y} KR_{Y,I,L_{c,m}} \times (n_Y)^{-1} \quad (3).$$

Using the stock-related data summarized above, age-at-maturity (A), or proportion mature-at-age (U), length-at-maturity, and length-at-age were estimated within each year using samples collected from the spawning region (area 4X, excluding subarea 4Xs; Fig. 1). We did not have sufficient information to account for biases resulting from the possibility of spatial segregation among mature and immature fish. We also compared our estimates to those of Power et al. (2011) for age- and length-at-maturity aggregated over years, where the maturity ogive (age) was <3=0, 3=0.5, 4=0.9 and >4=1.

2.2.2. Estimation of E and SSB

Number-at-age estimates for each year (Y; $N_{A,Y}$) were derived from a 2010 sequential population analysis, SPA (Power et al. 2011), that provided retrospective estimates to 1965 for ages 1 through 11+ . We restricted the analyses to the period 1970-2001 and estimates of E were determined as in Óskarsson and Taggart (2010). First, we estimated the number mature-at-age (m) for each year:

$$N_{m,A,Y} = N_{A,Y} \times U_{A,Y} \times H_A \quad (4)$$

where the proportion of females (H) in the stock was derived from Power and Iles (2001) and ranged from 0.49 to 0.6 (youngest to oldest). We then estimated the average L (cm) for all age groups for each year (1970 through 2001). Subsequently, the average length-at-age for each year was incorporated into the fecundity relation (modified F_P as function of L; see results) to calculate annual egg production, E_Y:

$$E_Y = \sum_{i=1}^{A} F_{\text{P},L} \times N_{m,L,Y} \quad (5).$$

Estimates of the annual contributions to E by the recruit (*rec*) and repeat (*rep*) spawners were then determined as follows;

$$E_{\text{rep},Y} = \sum_{i=1}^{A} \left(\frac{U_{Y-1,A-1}}{U_{Y,A}} \times E_{Y,A} \right) \quad (6)$$

where $E_{\text{rec},Y} = E_Y - E_{\text{rep},Y}$, and where the recruit spawners are typically age-4. In addition, E was estimated as in eq. 5 above using the previously determined fecundity relationship for the stock (below).

Annual spawning stock biomass (SSB_Y) estimates were calculated in the conventional manner by summing over each year the stock number-at-age multiplied by average weight-at-age (W_A; Power et al. 2011) and the proportion of mature individuals:

$$\text{SSB}_Y = \sum_{i=1}^{A} N_{A,Y} \times W_{A,Y} \times U_{A,Y} \quad (7).$$

The annual estimates of E using the F_P relationship for 2001 (including L and K) were compared to the annual SSB estimates for the stock, where each is based on the number-at-age from the SPA and the year-specific maturity ogive; the differences being due to the fecundity relationship, the sex ratio (restricted to the E estimation; eq. 4 and eq. 5), and the weight-at-length relationship (restricted to the SSB estimates; eq. 7).

2.2.3. Comparison with historical fecundity data

Historical fecundity relationships for the SFS stock were obtained from two sources. The first was Messieh (1976) based on 243 individuals at maturity stage-4 or -5 collected in 1970 and 1972 that provided an estimate of F_P as a function of L: $\log_2 F_P$ [thousands]= −22.71 + 4.75 $\log_2 L$ [mm] (r^2=0.66). The second from Perkins and Anthony (1969) was based also on 243 fish collected in 1963 and 1964 at maturity stage-5 but few at stage-4. We determined a linear relation based on a graphical extraction of the data provided in Figure 3 of Perkins and Anthony (1969): $F_P = 1.19\times10^4 L$ [cm] − 2.70×10^5 (r^2=0.527, p<0.001, n=265). The effects of using different F_P-at-length relationships in estimations of the total egg production were examined by using the two historical fecundity relationships in eq. 5.

2.3. STATISTICAL METHODS

F_P was assessed using least squares linear regression employing the appropriate transformations, generally $\log_{10}$. Standardized residuals were examined to determine statistical outliers and to validate homogeneity of variance assumptions. Quantiles of the residuals were used to assess normality. Stepwise regression (forward and reverse), employing the Mallow's C_P statistic (Neter et al. 1996) as a measure of goodness-of-fit, was used where more than one explanatory variable was considered. Model improvements were evaluated on the basis of approximate F–tests (Hastie and Tibshirani 1990). Because assumptions of normality and homogeneity of variance were not met for analyses of temporal changes in the maturity ogive (proportions) of the different length classes, GLM (Generalized linear models) logistic regression was used. Significance was considered at α=0.05. Different estimates of E were compared using the non-parametric Wilcoxon Signed-rank test.

3. RESULTS

3.1. FECUNDITY

The one hundred female herring collected in September 2001 were all at maturity stage-5 (fully mature). Total length ranged from 23.6 to 34.1 cm and the weight-at-length relation reflected near-isometric growth ($W=2.06\times10^{-3} L^{3.43}$ [cm], n=100, r^2 between fitted and observed estimates = 0.958, p<0.001; Fig. 2a). F_P increased linearly with total length ($F_P=1.37\times10^4 L - 3.05\times10^5$, r^2 between fitted and observed estimates = 0.894, n=100, p<0.0001) with an intercept at 22.3 cm (Fig. 2b). F_P was also strongly related to W ($F_P=2.48\times10^5\times\log_{10} W - 4.82\times10^5$, r^2 between fitted and observed estimates = 0.903, n=100, p<0.0001; Fig. 2c). Combining the weight-at-length relation and the aggregated F_P-at-length relation allowed the analytical derivation of a strong F_P-at-weight relationship ($F_P = 1.37\times10^4 (W\ 0.00206^{-1})^{1/3.43} - 3.05\times10^5$), which was highly correlated with predicted F_P from W (r=0.999; Fig. 2c). Each of the above relations is remarkably similar to those determined for Icelandic summer spawning herring (ISS; Óskarsson and Taggart 2006, Figures 6, 7 and 8 respectively), though the length and weight estimates for the SFS herring (maximum 34 cm, 340 g) are truncated relative to ISS herring (maximum 39 cm, 500 g); i.e., the size structure is markedly different between the two.

Residuals from the F_P-at-length relationship (Fig. 2b) were a weak and positive function of Fulton's K ($F_{P,resid}$ =56.44 K -49.65; r^2=0.10, n=100, p<0.01; Fig. 3). Hence, K explained 1.8% of the variation in F_P relative to L using multiple least square regression (F_P [$\times10^3$] = 12.00×L [cm] + 98.82×K -341.9, r^2=0.912, p<0.0001). Length and K explained

slightly more of the variation in F_P than did the non-linear function of W (Fig. 2c; approximate F-tests: p=0.002), but slightly less than the linear function of W (F_P [$\times 10^3$] = 0.548$\times W$ [g] - 27.9, r^2=0.919, p<0.0001); approximate F-tests: p=0.007). However, the former relationship (F_P as a function of L and K) is preferred when estimating E (below) as L estimates (i.e., number-at-length) are more readily available than W estimates from survey data and L does not vary seasonally as much as W. K can then easily be obtained as a seasonal average. Relative fecundity increased with L (RF_P=751-$e^{9.08-0.127\ L}$; r^2 between fitted and observed estimates=0.606, n=100, p<0.0001; Fig. 4) with the intercept at 19.7 cm. When the intercept was forced to 22.0 cm, approximating the smallest size for maturity within the stock data, the relation was similar and slightly weaker (RF_P=154$\times$(L-22)$\times e^{-0.0971 \cdot L}$; r^2=0.561, p<0.0001).

3.2. TOTAL EGG PRODUCTION

3.2.1. Body condition and stock specific biological variables

Fulton's K estimates for fully mature spawners (stage-5) collected in 2001 (n=100) ranged from 0.71 to 1.04 with an equivalent mean and median of 0.857 (Fig. 5a). The range in K for fully mature herring collected during 1972 through 2001 (n=9,175; 1970 and 1971 excluded due to few data) was 0.66 to 1.13 (statistically defined outliers withheld) and the mean of 0.906 and median of 0.907 were each greater than for the 2001 herring ($F_{1,\ 9\ 273}$=31.8, p<0.001; Fig. 5b). The time series of the annual average estimates of K for fully mature females revealed high interannual variation, with some evidence of a long-term downward trend in later years (Fig. 6a) that may be related to decreasing length-at-age (see below). The annual residuals around the average K calculated for the entire pre-spawning season (fish at maturity stage-3 to -5 inclusive) were equally variable among years (Fig. 6b) and were well correlated with the stage-5 estimates (serial cross-correlation, lag=0: r=0.825, n=29, p<0.0001). A comparison of the two series indicated a maximum difference of 4.1% (in 1992) and an average difference of 1.6%. Thus, the K-index (residuals + median=0.907) was chosen to represent the annual variation in K for the remaining analyses since it was available for all years during 1970 through 2001 and was based on a greater number of spawners (33,270) than the average K for stage-5 spawners (9,175).

Length-at-age significantly decreased over time ($\alpha \leq 0.05$) for ages 3+ but there was no trend for immature age-2 herring (Fig. 7a; Table 2a). Age and maturity data for 1981 were excluded due to data limitations in area 4X (Fig. 1). The proportion mature-at-age showed considerable variation in the age-3 herring throughout the period (Fig. 7b) and 1999 was anomalous with the lowest proportion mature at age-3 and -4. When pooled across all years, the percentages mature-at-age-2, -3, -4, and -5 were; 0.2 (SD=0.1), 38 (SD=17), 91 (SD=8), and 99% (SD=3) respectively, and comparable to the analyses of Power and Iles (2001). The time-series indicated that age-at-maturity for age-3 has fluctuated throughout the period while age-4 fish were consistently ≥90% mature after 1981 (except 1999) and age-5 were ≥96% mature after 1973; each showing a significant increasing linear trend (arc-sin square root transform, p=0.001 and p=0.005, respectively) over the series. The proportion mature-at-length fluctuated more so than by age (Fig. 7c) though each length class showed a significant increasing trend with time (Table 2b). Figure 7 and Table 2 illustrate that ages 3+ SFS herring have been decreasing in size-at-age and maturing at a smaller size over time, while a similar trend is not apparent in the age-2 herring.

3.2.2. Estimation of E and SSB

Total egg production, E, estimated using year-specific age-at-maturity (eq. 5), was strongly related to estimates based on a fixed age-at-maturity (Power et al. 2011; r^2=0.965) and with a zero intercept (p=0.838). The relation between estimates of SSB (eq. 7) using year-specific age-at-maturity and a fixed age-at-maturity was also strong (r^2=0.929) with a zero intercept (p=0.689). SSB estimates based on a fixed age-at-maturity were on average 2.5% greater than SSB based on varying age-at-maturity, with 29% higher estimates in 1973 and ~10% higher in 1970, 1979, and 1999 but 11% and 10% lower in 1986 and 2000, respectively. Because of the strong correlation between the two SSB estimates (fixed and varying age-at-maturity) we chose to employ the varying age-at-maturity estimates in subsequent analyses as they reflect the measurable inter-annual variation.

Estimates of E, determined using F_P as a function of total length and K (3.1 above) were different from the estimates based on F_P as function of length only (Wilcoxon Signed-rank test; n=32, p<0.0001), although the two were strongly correlated (r^2=0.987, p<0.001). The underestimation of E based on length only was >15% in three years (1980, '85, and '97) and averaged 5.2% less across all years. Overestimation occurred in seven years and was at a maximum 5.6% in 1978. These comparisons emphasize the significance of K in the F_P-analyses and indicate the F_P-relationship (i.e., $F_P \sim L+K$) in the annual calculations of E (eq. 5) should be used for comparisons with annual variation in SSB.

There was a strong correlation between the SSB and E (Fig. 8; $\log_{10} E\ (10^9) = 1.001 \times \log_{10}$ SSB [tonnes] -0.531; r^2=0.977, n=32, p<0.001). Underestimation of E based on prediction from the relation was most pronounced in 1979 at 9.3×10^{12} eggs, or ~18% greater E than expected and over 10% in 1973, 1985 and 1995. In 1981, 1998 and 2000, E was 14 to 18% lower than predicted. Overall, the under- and over-estimates using SSB averaged 6.2 and 6.1% respectively with a 95% prediction interval ranging from $\pm5\times10^{12}$ to 36×10^{12} eggs for the highest SSB (Fig. 8).

Annual total egg production was often dominated by a single strong year class, (sometimes by more than an order of magnitude, e.g., the 1970-year class), or by several intermediate year classes, (e.g., the 1976, '82, and '83 year classes) and most often the age-4 herring, the recruit spawners, contributed the greatest proportion to total egg production (Fig. 9). Consequently, there were pronounced fluctuations in the relative contribution to the total egg production by recruit and repeat spawners (Fig. 10a) such that the proportion of total egg production from recruit spawners fluctuated frequently (on average every 5 years) over a range of 13 to 56%. Although the percentage of SSB derived from recruit spawners (Fig. 10b) differed (Wilcoxon Signed-rank test on arc-sin of square root transformed data; Z=3.32, n=31, p<0.001) from the percentage of E derived from recruit spawners (Fig. 10a), the two estimates were strongly correlated (r=0.970). Moreover, during the 31 year period, the age composition of the stock varied somewhat systematically with fewer fish in the oldest age groups during the first 5 and most recent 15 years, each associated with fewer fish at increasing age (greater negative slopes; Table 5) indicating a truncated age distribution in the stock for those years (Fig. 11).

3.2.3. Comparison with historical fecundity data

F_P-at-length determined for 2001 was greater than F_P-at-length (and at-weight) reported for 1970 by Messieh (1976; Table 3, combined subarea 4Xo, n=46; 4Xq, n=95; and 4Xr, n=102; see subareas in Fig. 1), however, in 1970, F_P differed among areas. When

comparing data only from subarea 4Xq (the area where ovaries were collected in our study; Fig. 1), the 1970 length specific F_P estimates were similar to those from 2001 for females with K ranging from 0.80 to 0.85 (Table 3). The per cent variation in F_P explained by total length was greater in 2001 (91%) than in 1970 (74% subarea 4Xq; 66% all areas). Although weight-at-length was not provided by Messieh (1976), we were able to provide estimates for the different length groups in subareas 4Xq and 4Xr and all areas sampled in 1970 by combining the two equations (F_P at L = F_P at W) that describe F_P in 1970 and thus estimate weight-at-length (Table 4). Equivalent analyses of the 2001 samples were used for comparison. Weight-at-length was greater in 2001 than in 1970 for all areas and for subarea 4Xq only. We emphasize that the 1970 samples were primarily collected in July and August and most likely from Trinity Ledge, the predominant fishing area in that period, whereas our estimates for 2001 were based on samples at the same maturity stage but from nearby German Bank and collected in September. Relative fecundity estimates, normalized by whole body weight (historical ovary weight not available), were also highest in 2001 and lowest in area 4Xr in 1970 (Table 4).

For 1963 and 1964, Perkins and Anthony (1969) provided limited fecundity analyses of 243 individuals from the stock in the form of an unspecified linear F_P-at-length relationship within a scatter plot of their observations. The relationship derived from the graph they provided was comparable to F_P-at-length in 1970 (aggregate data) and more variable and lower than that observed in 2001 (Table 3). Thus, the results of these F_P-at-length comparisons challenge the assumption of temporal stability in fecundity relations.

For further comparisons, the different F_P-at-length relations (1963, 1964, 1970s, and 2001) were used to estimate the annual total egg production of the stock. Figure 10c shows that when age-at-maturity and sex-ratio were constant there was a difference between the estimates of E based on the F_P relationships from 2001 (including L and K) and the estimates of E based on the length-F_P relationships obtained from Perkins and Anthony (1969; Wilcoxon Signed-rank test; n=32, p<0.0001) and Messieh (1976; Wilcoxon Signed-rank test; n=32, p<0.0001). The annual estimates of E based on the 2001 F_P determinations were on average 1.3 fold greater than both the estimated E using the Messieh (1976) F_P relation (SD 0.068) and that estimated using the Perkins and Anthony (1969) F_P relationship (SD 0.066). However, despite the differences in the absolute annual estimates of E, they are all strongly correlated (r ranging from 0.994 to 0.999).

4. DISCUSSION

The results of our analyses show that the annual estimates of E for the SFS herring stock are closely related to the SSB estimates for both the recruit and repeat spawners. This indicates that while E is generally considered to be a preferable approximation (Rijnsdorp 1994; Marshall et al. 1998; Cardinale and Arrhenius 2000; Marshall 2009; Óskarsson and Taggart 2006; 2010), it is not likely to provide a statistically meaningful improvement in explained recruitment variation relative to SSB. However, partitioning the reproductive potential between recruit and repeat spawners (Fig. 10a and 10b), or among different age-classes (Fig. 9) as done here, is still relevant when assessing recruitment variation. This relevance lies in the fact that eggs from recruit spawners are considered to be of a lesser quality in terms of size, growth rate and survivorship than eggs derived from the larger and older repeat spawners (Blaxter and Hempel 1963; Hislop 1988; Kjesbu et al. 1996; Sogard et al. 2008; see Óskarsson 2005 for more refs.) and is manifested for SFS herring in a positive relationship between egg-

size and fish-size (Óskarsson 2005). Although the results imply that the maximum reproductive output in terms of egg quantity typically occurs at age-4 (Fig. 9), the 'true' maximum reproductive output, when accounting for egg quantity and quality etc. (as above), could be at age-5 or older. This is the same age (5) that Rosenberg and Doyle (1986) concluded would have maximum total reproduction output for the same stock when calculated using the gonad weight to length relationship, weight-at-age data, and number of mature females.

The results of our analyses indicating that E is proportional to SSB were unexpected for several reasons. First, relative fecundity (RF_P) is apparently a function of total length and this would suggest that the length composition of the stock should disproportionately influence E relative to SSB. Second, F_P was found to be a weak function of K (Fig. 3), indicating that annual variation in K is reflected in E in a manner different from that reflected in the SSB estimates. These results for SFS herring are consistent with results derived from Icelandic summer-spawning (ISS) herring analyses (Óskarsson and Taggart 2006; 2010), North Sea herring (Kell et al. 2016) and Norwegian spring-spawning herring (Ndjaula et al. 2010), where there was also a strong correlation between E and SSB. As the length-specific F_P variation is relatively small and the annual variation in number of spawners is large for the SFS and ISS herring stocks, the influence of F_P appears minimal; i.e., variation in E is relatively unaffected by changes in F_P. This is manifest in a strong linear relationship between F_P and W (r^2=0.919) comparable to the non-linear relationship (r^2=0.903); equivalent to the observed proportionality between E and SSB. Moreover, the effects of K on F_P appears small at the stock level for SFS herring since K, in addition to fish length, explained a comparable amount of the variation in F_P (r^2=0.912) as weight alone (see above, depending on linear or non-linear relationship). Consequently, these results, as well as those of McIntyre and Hutchings (2003), provide little evidence that spawner condition, at least as measured using Fulton's K near spawning, has a measurable influence on F_P. Thus, any small variation in fecundity at the individual level due to, for example, varying K, appears to have minimal influence when integrated across the stock. This is the case not only for SFS and ISS herring (Óskarsson and Taggart 2006; 2010) but also for Baltic cod (*Gadus morhua*; Tomkiewicz et al. 1997), NW-Atlantic cod, and three flatfish species (Rideout and Morgan 2010). This allows us to conclude that the approximation of proportionality between E and SSB in stock-recruitment relationships is valid, particularly for herring.

Our results do raise concerns as to whether K adequately reflects the individual energetic condition for herring as has been indicated by others for cod (Marshall et al. 2004; Koops et al. 2004). Studies by McPherson et al. (2011) indicated a relationship between K and fat measurements for pre-spawning herring (r^2 ranging from 0.13 to 0.35) even if weaker than for immature herring (r^2=0.52). They concluded that K might not be a proxy of fat *per se*, but a proxy of the health of an individual, which corresponds to the Ndjaula et al. (2010) conclusion that K is a proxy for the stock condition. Similarly, post-spawning Icelandic herring show that K is related to fat content and is therefore a valid index of energetic condition during that part of the annual cycle but less so during the pre-spawning season (Óskarsson 2008). It has been suggested that there are other factors that reduce the strength of the relation between fecundity and body condition. For example, the timing of the fecundity determination affects the relation due to the down-regulation of fecundity over a given period during the pre-spawning season (van Damme et al. 2009; Kennedy et al. 2011); i.e., fecundity is reduced and adjusted to the fish condition during the pre-spawning period by means of atresia. We have earlier shown that mesenteric fat content in herring falls off precipitously with increasing ovary weight as

spawning time approaches (Óskarsson and Taggart 2009). Condition at the beginning of ovary development might be crucial in influencing the effect of condition on fecundity at some later time closer to spawning; i.e., earlier (months) condition might be correlated with fecundity just prior to spawning. Correspondingly, condition observed just prior to spawning might not reflect an earlier condition for a variety of reasons (Kennedy et al. 2011). In this study, fecundity and K were determined just prior to spawning and the K estimates of the fish used for determining fecundity were representative from an historical perspective (Fig. 5, 6) and are remarkably similar to those determined for Icelandic summer-spawning herring (Óskarsson and Taggart 2010; Fig. 5, 4). Thus, the effects of K on F_P could be underestimated in our study due to collection of fish for fecundity estimates just before spawning even though we assumed that our fish reflect the full biological range of the stock in terms of body condition (Fig. 5). It must be noted that individual herring in extremely poor body condition (K<0.7) have been found to have high intensity of atresia likely resulting in absorption of eggs and no spawning (Óskarsson et al. 2002) but at the stock level such individuals are apparently rare (Fig. 5; Óskarsson and Taggart 2010) with a generally insignificant impact on E.

Our results indicate a long-term decrease in the age-at-maturity over the 32-year study period, a decrease in length-at-maturity, and a decrease in size-at-age (Fig. 7, Table 2). We also show a decrease in the proportion of the older (larger) age classes (Fig. 11, Table 5) and thus a reduced contribution to total egg production (Fig. 9). These patterns are consistent with an emergent property for a stock subject to a size-selective fishery; a fishery that preferentially targets the larger (older) and faster growing and late maturing individuals. Observations of such maturation trends (i.e., maturation at earlier age and smaller size) have been suggested as a warning, signaling a less sustainable population (Olsen et al. 2004; Melvin and Stephenson 2007; Neuheimer and Taggart 2010). Furthermore, it is clear from Figure 11 that from a demographic perspective (number-at-age) the stock has contained relatively fewer older fish in the most recent 15 years of data (1996-2009) than in the previous three decades and that the number of fish at age-9 and -10 fall below 2 million and the age 10 fish fall below 500 thousand in the most recent years; something not previously observed except in the mid 1960s. Thus, there are indications, both from historical analyses of age-at-maturity and recent age composition of the stock, that the stock has reduced productivity in recent years.

Decreased age- and length-at-maturation can also have evolutionary consequences resulting from selective fisheries that target larger (fast growing, late maturing) individuals in the stock (e.g., Gadgil and Bossert 1970; Engelhard and Heino 2004b, Ernande et al. 2004; Olsen et al. 2004; Hutchings 2004; Wheeler et al. 2009). However, there are indications that changes in age- and length-at-maturity are reversible, at least for herring (Beverton 2002; Engelhard and Heino 2004a; Óskarsson and Taggart 2010), suggesting phenotypic plasticity (Enberg et al. 2012). The clear trends for SFS herring throughout the 32-year period in increasing age- (Fig. 7b) and length-at-maturity (Fig. 7c and Table 2b) and decreasing length-at-age (Fig. 7a and Table 2a), the latter consistent with the observations of Power and Iles (2001), are different from ISS herring that show no such trends over a similar period (Óskarsson and Taggart 2010). There is no clear single explanation for the difference. Although the SFS and ISS fisheries use generally the same gear (purse seine), the Icelandic fishery is prosecuted prior to and during the overwintering period while most of the SFS fishery is prosecuted prior to and during spawning and at times included a directed roe fishery. However, relatively non-size-selective fishing gears, such as purse seine, can contribute to selectivity of fishery through the fishing pattern when fleets are targeting earlier and older spawners in contrast to later and younger spawners, because older herring spawners tend to

spawn earlier than younger spawners (Lambert 1987; Slotte et al. 2000; Óskarsson and Taggart 2009). We suggest that such changes in life-history traits observed in the SFS herring are related to earlier maturation because the somatic growth rate declines when a fish matures. This means that the ratio of reproductive investment (somatic growth)$^{-1}$, in terms of expenditure of the total consumed energy per fish, has on average increased over the period. Whether this might be reflected in recruitment variability has yet to be determined although there have been no big year classes since the 1983 year class recruited to the stock (Singh et al. 2014).

The differences observed in length-specific F_P relations of the SFS herring can affect the reproductive potential without affecting SSB (e.g., Marshall et al. 1998). The observed difference in length-specific F_P may be related to stock density, because the relative fecundity was higher in 2001 than in 1970 (Table 4) while the SSB was lower in 2001 (Fig. 10b). An inverse relation between fecundity and SSB, as is the case here, can be expected where fecundity is density dependent as has been suggested for herring, cod and other species (Kelly and Stevenson 1985; Stares et al. 2007 and refs. therein). Furthermore, no difference was found in fecundity for Norwegian spring-spawning in years of similar SSB but ~45 years apart with an intervening stock collapse (Ndjaula et al. 2010). However, there are at least four possible explanations that could account for the apparent temporal variation in SFS herring F_P: (1) heritable genotypic or phenotypic changes in the stock, i.e., more fecund-at-size at present possibly due to stock density; (2) our analyses assume one stock when subunits of the stock complex (Stephenson et al. 2009) may have different characteristics; (3) different methods used in determining F_P; and (4) more variation in the F_P estimates in the historical data as evidenced by the data and results (Table 3). While, according to our data and information, we are unable to unambiguously reject any of the above four alternative explanations for the temporal difference in length-specific F_P (see Óskarsson 2005), we rest on the assumption that applying the fecundity relationship obtained in 2001 provides the best approximation of total annual egg production until such time as more comprehensive data become available. Yet another theoretical explanation for the difference in the F_P estimates is related to the timing of ovary sampling with respect to the spawning time. As pointed out above, fecundity of herring is down-regulated during the pre-spawning season (Kurita et al. 2003; Óskarsson and Taggart 2006; van Damme et al. 2009; Kennedy et al. 2011) and moreover, the spawning time of SFS herring is protracted over two months (related to point 2 above; Óskarsson 2005) in contrast to the relatively uniform and contracted spawning of Icelandic summer-spawning herring (Óskarsson and Taggart 2009). However, considering that the F_P estimate in 2001 was higher and based on ovaries collected, at least on average, closer to spawning (maturity stage-5) than in 1970 (maturity stage-4 and -5) and the annual residuals of K were higher in 1970 than 2001 (Fig. 6b), down-regulation is seemingly not responsible for the difference. Thus we conclude that the temporal differences in F_P cannot be easily explained.

Some general conclusions can be drawn from this study and the literature reviewed here. In relation to our main objective, we conclude that the approximation of proportionality between E and SSB in stock-recruitment relationships is valid, at least for herring. It means that applying E instead of SSB in determining biological reference points aimed for fishery management has insignificant statistical meaning. This is partly consistent with Kell et al. (2015), who found no improvements in stock-recruitment relationships for North Sea herring, cod and plaice (*Pleuronectes platessa*) by using E instead of SSB. They argued, however, that using E would improve the realism in the understanding of the stock dynamic. In a similar way, we argue that partitioning the reproductive potential in terms of SSB or E, between

recruit and repeat spawners or among different age-classes is relevant when assessing recruitment variation. Consequently, biological reference points aimed for fishery management based on stock-recruitment relationships where SSB is derived from repeat spawners instead of total SSB is more adequate for these stocks, and should be considered thoroughly. Temporal differences in F_P, as observed in this study, need further attention in the future because if valid they challenge the proportionality approximation between E and SSB over the long term.

5. ACKNOWLEDGEMENTS

We are grateful to M Power and others at the St. Andrews Biological Station for assistance with ovary collections and the historical data, A Barney and A Pickle for lab assistance, T Marshall, K Frank, and G Marteinsdottir for critical appraisals of an earlier draft, C Pampoulie and D Morin for translation of the abstract, and three anonymous referees who contributed to several improvements in the manuscript. Research support was provided by a Natural Sciences and Engineering Research Council Discovery grant to CTT, a North Atlantic Treaty Organisation Science Fellowship and Icelandic Research Fund Fellowship to GJO, the Marine Research Institute in Iceland, and the Fishery Ministry of Iceland.

6. REFERENCES

Anonymous 1962. Recommendations adopted by the Herring Committee. Rapp. P.-V. Re´un. Cons. Int. Explor. Mer. 1: 1–73. [Append.]

Bailey, R.S. and Almatar, S.M., 1989. Variation in the fecundity and egg weight of herring (*Clupea harengus* L.), part II. Implications for hypotheses on the stability of marine fish populations. J. Cons. Int. Explor. Mer 45: 125–130.

Beverton, R.J.H., 2002. Fish population biology and fisheries research, in Anderson, E.D. (Ed.), The Raymond J.H. Beverton lectures at Woods Hole, Massachusetts. Three lectures on Fisheries Science given May 2-3, 1994. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-F/SPO-54, pp. 61–105.

Beverton, R.J.H. and Holt, S.J., 1957. On the dynamics of exploited fish populations. Fishery Invest., London, Series 2, vol. 19. 533 pp.

Blaxter, J.H.S., and Hempel, G., 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Perm. Int. Explor. Mer. 28: 211–240.

Bowers, A.B., and Holliday, F.G.T., 1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). Marine Research 5: 1–16.

Cardinale, M., and Arrhenius, F., 2000. The relationship between stock and recruitment: are the assumptions valid? Mar. Ecol. Prog. Ser. 196: 305–309.

Cushing, D.H., 1988. The study of stock and recruitment. *In*,Fish populations dynamics: the implications for management. Edited by J.A. Gulland. John Wiley & Sons Inc., Chichester, UK., pp. 105–128.

van Damme, C.J.G., Dickey-Collas, M., Rijnsdorp, A.D., and Kjesbu, O.S., 2009. Fecundity, atresia, and spawning strategies of Atlantic herring (*Clupea harengus*). Can. J. Fish. Aquat. Sci. 66: 2130–2141.

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S., and Heino, M., 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar. Ecol. 33: 1–25.

Engelhard, G.H. and Heino, M., 2004a. Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. Fish. Res. 66: 299–310.

Engelhard, G.H., and Heino, M., 2004b. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? Mar. Ecol. Prog. Ser. 272: 245–256.

Ernande, B., Dieckmann, U., and Heino, M., 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. P. Roy. Soc. B-Biol. Sci. 271: 415–423.

Gadgil, M. and Bossert, W., 1970. Life historical consequences of natural selection. Am. Nat. 104: 1–24.

Hastie, T. and Tibshirani, R., 1990. Generalized additive models. Chapman & Hall, London. 325 pp.

Hislop, J.R.G., 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. J. Fish Biol. 32: 923–930.

Hutchings, J.A., 2004. The cod that got away. Nature 428: 899–900.

Kell, L.T, Nash, R.D.M., Dickey-Collas, M., Mosqueira, I., and Szuwalski, C., 2015. Is spawning stock biomass a robust proxy for reproductive potential? Fish and Fish. Doi: 10.1111/faf.12131

Kelly, K.H. and Stevenson, D.K., 1985. Fecundity of Atlantic herring (*Clupea harengus*) from three spawning areas in the western Gulf of Maine, 1969 and 1982. J. Northw. Atl. Fish. Sci. 6: 149–155.

Kennedy, J., Nash, R.D.M., Slotte, A., and Kjesbu, O.S., 2011. The role of fecundity regulation and abortive maturation in the reproductive strategy of Norwegian spring-spawning herring (*Clupea harengus*). Mar. Biol. 158: 1287–1299.

Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M., 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 53: 610–620.

Koops, M.A., Hutchings, J.A., and McIntyre, T.M., 2004. Testing hypotheses about fecundity, body size and maternal condition in fishes. Fish and Fish. 5: 120–130.

Kurita, Y., Meier, S., and Kjesbu, O.S. 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. J. Sea Res. 49: 203–219.

Lambert, T.C., 1987. Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. Mar. Ecol. Prog. Ser. 39: 209–220.

Mackinson, S., Vasconcellos, M., and Newlands, N., 1999. A new approach to the analysis of stock-recruitment relationships: "model-free estimation" using fuzzy logic. Can. J. Fish. Aquat. Sci. 56: 686–699.

Marshall, C.T., 2009. Implementing information on stock reproductive potential in fisheries management: the motivation, challenges and opportunities. *In* Fish reproductive biology: implications for assessment and management.Edited by T. Jakobsen, M.J. Fogarty, B.A. Megrey, and E. Moksness. John Wiley and Sons, pp. 395–420.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, Ø., 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? Can. J. Fish. Aquat. Sci. 55: 1766–1783.

Marshall, C.T., Needle, C.L., Yaragina, N.A., Ajiad, A.M., and Gusev, E., 2004. Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. Can. J. Fish. Aquat. Sci. 61: 1900–1917.

McIntyre, T.M., and Hutchings, J.A., 2003. Small-scale temporal and spatial variation in Atlantic cod (*Gadus morhua*) life history. Can. J. Fish. Aquat. Sci. 60: 1111–1121.

McPherson, A., Stephenson, R., O'Reilly, P., Jones, M., and Taggart, C.T., 2001. Genetic diversity of coastal Northwest Atlantic herring populations: implications for management. J. Fish Biol. 59 (Suppl.A): 356–370.

McPherson, A.A., Stephenson, R.L., and Taggart, C.T., 2003. Genetically different Atlantic herring *Clupea harengus* spawning waves. Mar. Ecol. Prog. Ser. 247: 303–309.

McPherson, L.R., Slotte, A., Kvamme, C., Meier, S., and Marshall, C.T., 2011. Inconsistencies in measurement of fish condition: a comparison of four indices of fat reserves for Atlantic herring (*Clupea harengus*). ICES J. Mar. Sci. 68: 52–60.

Melvin, G.D., and Stephenson, R.L., 2007. The dynamics of a recovering fish stock: Georges Bank herring. ICES J. Mar. Sci. 64: 69–82.

Messieh, S.N., 1976. Fecundity studies on Atlantic herring from the Southern Gulf of St. Lawrence and along the Nova Scotia coast. T. Am. Fish. Soc. 3: 384–394.

Ndjaula, H.O.N., Nash, R.D.M., Slotte, A., Johannessen, A., and Kjesbu, O.S., 2010. Long-term changes in the total egg production of Norwegian spring-spawning herring *Clupea harengus* (L.) Implications of variations in population structure and condition factor. Fish. Res. 104: 19–26.

Neter, J., Kutner, M.H., Nachtsheim, C.J., and Wasserman, W., 1996. Applied Linear Statistical Models, 4th edn. Boston: WCB/McGraw-Hill, 1408p.

Neuheimer, A.B., and Taggart, C.T., 2010. Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? Can. J. Fish. Aquat. Sci. 67(5): 854–865.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., and Dieckmann, U., 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428: 932–935.

Óskarsson, G.J., 2005. Pre-spawning factors and recruitment variation in Atlantic herring (Clupeidae; *Clupea harengus*, L.): A comparative approach. Thesis (PhD) Oceanography Department, Dalhousie University, Halifax, N.S., Canada. 251 pp.

Óskarsson, G.J., 2008. Variation in body condition, fat content and growth rate of Icelandic summer-spawning herring (*Clupea harengus* L.). J. Fish Biol. 72:2655–2676.

Óskarsson, G.J., Kjesbu, O.S., and Slotte, A., 2002. Predictions of realised fecundity and spawning time in Norwegian-spring spawning herring (*Clupea harengus*): possible implications for subsequent recruitment. J. Sea Res. 48: 59–79.

Óskarsson, G.J., and Taggart, C.T., 2006. Fecundity variation in Icelandic summer-spawning herring and implications for reproductive potential. ICES J. Mar. Sci. 63: 493–503.

Óskarsson, G.J., and Taggart, C.T., 2009. Spawning time variation in Icelandic summer-spawning herring (*Clupea harengus* L.). Can. J. Fish. Aquat. Sci. 66: 1666–1681.

Óskarsson, G.J., and Taggart, C.T., 2010. Variation in reproductive potential and influence on Icelandic herring recruitment. Fish. Oceanogr. 19: 412–426.

Perkins, F.E. and Anthony, V.C., 1969. A note on the fecundity of herring (*Clupea harengus harengus* L.) from Georges Bank, the Gulf of Maine and Nova Scotia. ICNAF, Redbook, No. 3: 33–38.

Power, M.J. and Iles, T.D., 2001. Biological characteristics of Atlantic herring as described by a long-term sampling program. *In* Herring: Expectations for a new millennium. Edited by F. Funk, J. Blackburn, D. Hay, A.J. Paul, R. Stephenson, R. Toresen, and D. Witherell. University of Alaska Sea Grant, AK-SG-01-04, Fairbanks, pp. 135–153.

Power, M.J., Knox, D., and Melvin, G.D., 2011. 2010 Evaluation of 4VWX Herring. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/112: vi + 124p.

Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11: 559–623.

Rideout, R.M. and Morgan, M.J., 2010. Relationships between maternal body size, condition and potential fecundity of four north-west Atlantic demersal fishes. J. Fish Biol. 76: 1379–1395.

Rijnsdorp, A.D., 1994. Population-regulating processes during the adult phase in flatfish Neth. J. Sea Res. 32: 207–223.

Rosenberg, A.A., and Doyle, R.W., 1986. Analysing the effect of age structure on stock-recruitment relationships in herring (*Clupea harengus*). Can. J. Fish. Aquat. Sci. 43: 674–679.

Singh, R., Knox, D., Power, M.J., MacIntyre, A., and Melvin, G.D., 2014. 2013 Evaluation of Northwest Atlantic Fisheries Organization (NAFO) Divisions 4VWX Herring. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/056. v. 109 pp.

Shepherd, J.G., 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40: 67–75.

Slotte, A., Johannessen, A., and Kjesbu, O.S., 2000. Effects of fish size on spawning time in Norwegian spring-spawning herring. J. Fish Biol. 56(2): 295–310.

Sogard, S.M, Berkeley, S.A., Fisher, R., 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. Mar. Ecol. Prog. Ser. 360: 227–236.

Stares J. C., Rideout, R.M., Morgan, M.J., and Brattey, J., 2007. Did population collapse influence individual fecundity of northwest Atlantic cod? ICES J. Mar. Sci. 64: 1338–1347.

Stephenson, R.L., Lane, D.E., Aldous, D.G., and Nowak, R., 1993. Management of the 4WX Atlantic herring (*Clupea harengus*) fishery - an evaluation of recent events. Can. J. Fish. Aquat. Sci. 50: 2742–2757.

Stephenson, R.L., Melvin, G.D., and Power, M.J., 2009. Population integrity and connectivity in Northwest Atlantic herring: a review of assumptions and evidence. ICES J. Mar. Sci. 66: 1733–1739.

Tomkiewicz, J., Eriksson, M., Baranova, T., Feldman, V., and Ernst, P., 1997. Maturity ogives and sex ratios for Baltic cod: establishment of a data base and time series. ICES C.M. 1997/CC:20. 21 pp.

Wheeler, J.P., Purchase, C.F., Macdonald, P.D.M., Fill, R., Jacks, L., Wang, H., and Ye, C., 2009. Temporal changes in maturation, mean length-at-age, and condition of spring-spawning Atlantic herring (*Clupea harengus*) in Newfoundland waters. – ICES J. Mar. Sci. 66: 1800–1807.

7. TABLES

Table 1. Summary of the number of mature (maturity stage–3 to 7 inclusive) and immature (maturity stage–1 and 2) Scotia-Fundy summer- and autumn-spawning female herring collected over the period 1970 through 2001 (Source: Dept. of Fisheries and Oceans Canada, St. Andrews Biological Station herring database). Grand total, average and standard deviation (SD) are provided at the bottom of the table.

Year	No. mature	No. immature	Year	No. mature	No. immature
1970	161	558	1986	1,006	673
1971	310	816	1987	1,803	798
1972	242	357	1988	1,590	723
1973	716	2,431	1989	884	481
1974	2,480	1,697	1990	1,190	1,127
1975	2,105	2,101	1991	1,565	818
1976	3,516	2,478	1992	839	368
1977	5,549	1,423	1993	1,000	338
1978	2,480	883	1994	1,019	484
1979	1,554	1,371	1995	1,077	438
1980	2,873	1,203	1996	1,718	479
1981	99	444	1997	1,093	508
1982	3,410	1,310	1998	1,959	450
1983	2,706	1,219	1999	1,421	850
1984	3,727	1,914	2000	1,295	413
1985	2,273	1,019	2001	2,317	753
			N	32	32
			Total	55,977	30,925
			Average	1,749	966
			SD	1,188	607

Table 2. Least squares regression parameters for Scotia-Fundy summer- and autumn-spawning herring females for (**a**) length-at-age (in cm) and (**b**) proportion mature-at-length as a function of time (year) over the period 1970 through 2001 (logistic regression; see Figs. 7b and 7c): slope, and significance (*p*-value) and the coefficient of determination (r^2) between observed and fitted values.

a Age (years)	Slope (cm)	*p*-value	r^2	**b** Length (cm)	Slope (%) [1]	*p*-value	r^2
2	-0.011	0.72	-	22	0.33	<0.001	0.384
3	-0.048	0.015	0.182	23	1.43	<0.001	0.617
4	-0.053	0.003	0.252	24	2.27	<0.001	0.694
5	-0.069	<0.001	0.422	25	2.45	<0.001	0.746
6	-0.081	<0.001	0.810	26	1.70	<0.001	0.783
7	-0.071	<0.001	0.784	27	1.12	<0.001	0.799
8	-0.078	<0.001	0.823				

[1] The slope from the predictions from the logistic regression against the years providing the average increase over the period.

Table 3. The predicted potential fecundity (F_P; $\times 10^3$) for the different fecundity determination for the Scotia-Fundy summer- and autumn-spawning herring (SFS) where total length (L) is in cm and K the Fulton's condition factor (g cm^{-3}).

	F_P ($\times 10^3$) in year 2001 [1]			F_P ($\times 10^3$) in year 1970			
Length (cm)	K=0.75	K=0.85	K=0.95	Subarea 4Xq [2]	Subarea 4Xr [3]	All areas [4]	F_P ($\times 10^3$) in year 1963-64 [5]
25	37.8	43.9	50.2				28.0
26	44.8	52.0	59.5				39.5
27	52.7	61.3	70.0	56.1	42.2	49.8	51.5
28	61.8	71.8	82.0	66.2	51.2	59.2	63.5
29	71.9	83.6	95.5	77.6	61.8	69.9	75.5
30	83.3	96.8	110.7	90.5	74.1	82.1	87.5
31	96.1	111.6	127.6	105.0	88.3	96.0	99.5
32	110.3	128.1	146.4	121.3	104.6	111.6	111.5
33	126.0	146.4	167.3	139.5	123.4	129.1	123.0
34	143.4	166.7	190.5	159.7	144.7	148.7	
35				182.2	169.0	170.6	
36				207.0	196.5	195.0	
37				234.5	227.5	222.1	

[1] $\log_2 F_P = 4.34 \times \log_2 L$ [cm] $+ 1.20 \times \log_2 K - 9.99$; r^2=0.930, n=100; SE of parameters: 0.192, 0.222, and 0.669, respectively (this paper)

[2] $\log_2 F_P = 4.54 \times \log_2 L$ [cm] -10.94; gives $F_P \times 10^3$; r^2=0.740, n=95 (Messieh 1976)

[3] $\log_2 F_P = 5.35 \times \log_2 L$ [cm] -13.89; gives $F_P \times 10^3$; r^2=0.608, n=102 (Messieh 1976)

[4] $\log_2 F_P = 4.74 \times \log_2 L$ [cm] -11.72; gives $F_P \times 10^3$; r^2=0.656, n=243 (Messieh 1976)

[5] $F_P = 11.9 \times L$ [cm] -269.5; r^2=0.527, n=265; SE of parameters: 0.693, 22.2, respectively (extracted from Perkins and Anthony 1969).

Table 4. The predicted whole body weight (g) of Scotia-Fundy summer- and autumn-spawning herring during 1970 and 2001 by combine the potential fecundity-total length relationships ($F_{P,L}$; Table 3) and F_P-whole body weight (W; g) relationships, and the corresponding relative fecundity on whole body weight basis ($RF_{P,W} = F_P \times W^{-1}$).

	Predicted whole body weight (g)				$RF_{P,W}$ (g^{-1})			
Length (cm)	2001 [1]	1970, subarea 4Xq [2]	1970, subarea 4Xr [3]	1970, all [4]	2001	1970, subarea 4Xq	1970, subarea 4Xr	1970, all
27	163.5	163.8	157.8	159.9	363	342	267	304
28	186.4	184.4	179.6	181.4	383	359	285	318
29	211.5	206.8	203.5	204.9	403	375	304	333
30	239.0	231.0	229.7	230.5	423	392	323	347
31	268.9	257.2	258.2	258.2	443	408	342	362
32	301.5	285.2	289.2	288.3	464	425	362	377
33	336.8	315.4	322.7	320.7	485	442	382	393
34	375.0	347.7	359.0	355.7	507	459	403	408
35	416.3	382.2	398.1	393.3	528	477	425	423
36	460.7	419.1	440.1	433.7	550	494	446	439
37	508.4	458.3	485.3	476.9	572	512	469	455

[1] $\log_{10} W = 3.6 \log_{10} L$ [cm] -2.94 (this paper)
[2] $\log_2 W = 3.27 \log_2 L$ [cm] -5.67 (derived from Messieh 1976)
[3] $\log_2 W = 3.57 \log_2 L$ [cm] -6.68 (derived from Messieh 1976)
[4] $\log_2 W = 3.47 \log_2$ L [cm] -6.35 (derived from Messieh 1976).

Table 5. The statistic of linear regressions of number of Scotia-Fundy summer- and autumn-spawning herring (log_{10}-transformed) from an analytical assessment (Power et al. 2011) against their age (age 3 to 10) for every five years combined for the period 1966-2010.

Years	Intercept	Slope	r^2	p-value	n
1966-70	10.70	-0.377	0.822	<0.01	35
1971-75	9.60	-0.233	0.674	<0.01	35
1976-80	9.61	-0.266	0.600	<0.01	35
1981-85	10.43	-0.388	0.877	<0.01	35
1986-90	10.31	-0.300	0.804	<0.01	35
1991-95	9.27	-0.189	0.553	<0.01	35
1996-00	10.40	-0.421	0.949	<0.01	35
2001-05	10.11	-0.391	0.915	<0.01	35
2006-10	9.78	-0.339	0.819	<0.01	35

8. FIGURES

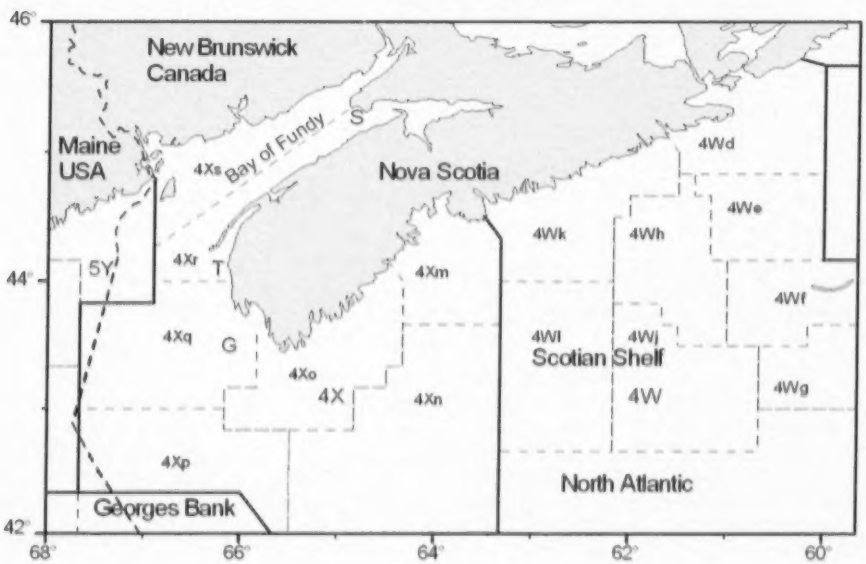

Figure 1. Chart showing sampling locations on German Bank (G), Trinity Ledge (T), and in Scot's Bay (S) in the Scotia-Fundy region of individual summer- and autumn-spawning herring collected during 1970 through 1999. Solid lines mark the boundaries of the statistical fishery units referred to in the text and the dotted line the subareas. The database contains information on samples collected from 4X (except for 4Xs) and 4W.

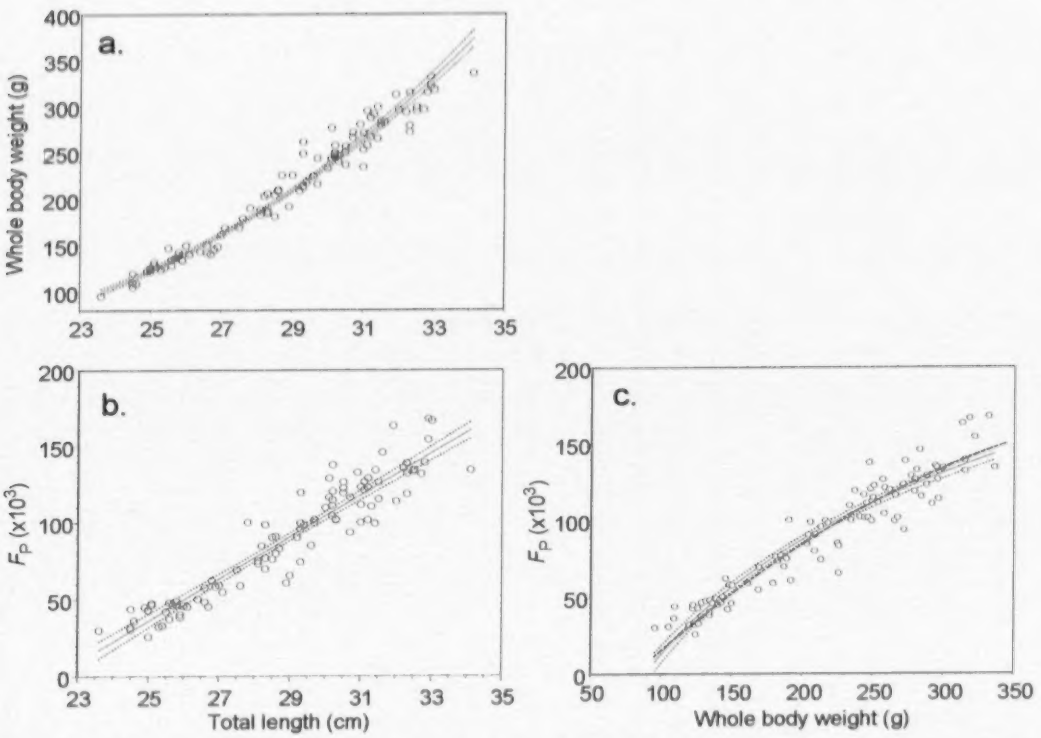

Figure 2. Scattergram of observations (open symbols) for Scotia-Fundy summer- and autumn-spawning herring collected in September 2001 and least squares regression (solid line) and 95% confidence interval (dotted lines) around the regressions showing: (a) whole body weight (W; g) as a function of total length (L; cm); (b) the potential fecundity (F_P; $\times 10^3$) as a function of L,; and (c) F_P as a function of W. The predicted relationship from weight-at-length and F_P-at-length is indicated with the broken line.

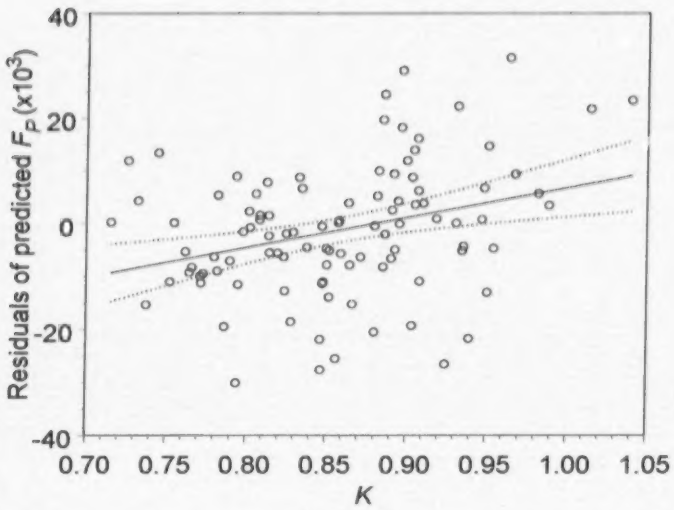

Figure 3. Scattergram of observations (open symbols) and least squares regression (solid line) and 95% confidence interval (dotted lines) around the regressions showing the residuals for potential fecundity ($F_{P,\ resid}$, $\times 10^3$) fitted using total length (see Figure 2b) as a function of Fulton's condition factor (K) for Scotia-Fundy summer- and autumn-spawning herring collected in 2001.

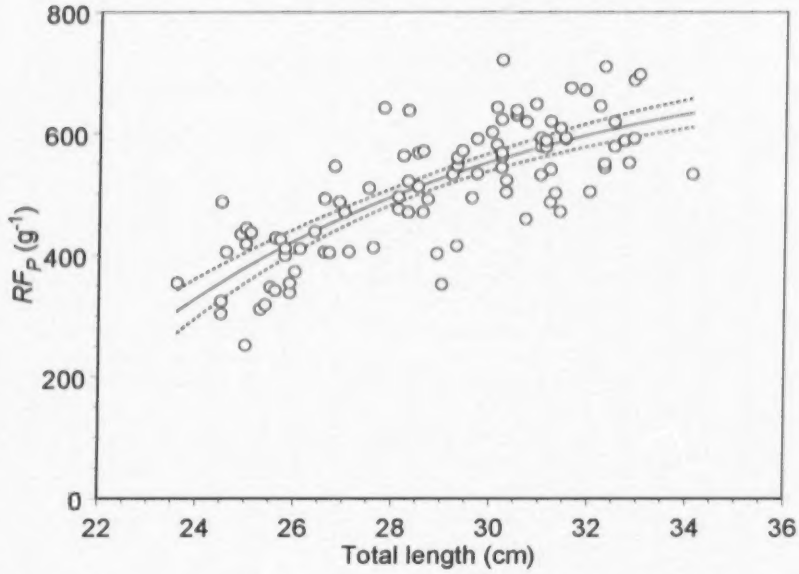

Figure 4. Scattergram of observations (open symbols) and least squares regression (solid line) and 95% confidence interval (dotted lines) around the regression showing the relative fecundity (RF_P= potential fecundity (whole body weight-ovary weight)$^{-1}$; g^{-1}) against total length (L; cm) of Scotia-Fundy summer- and autumn-spawning herring in 2001.

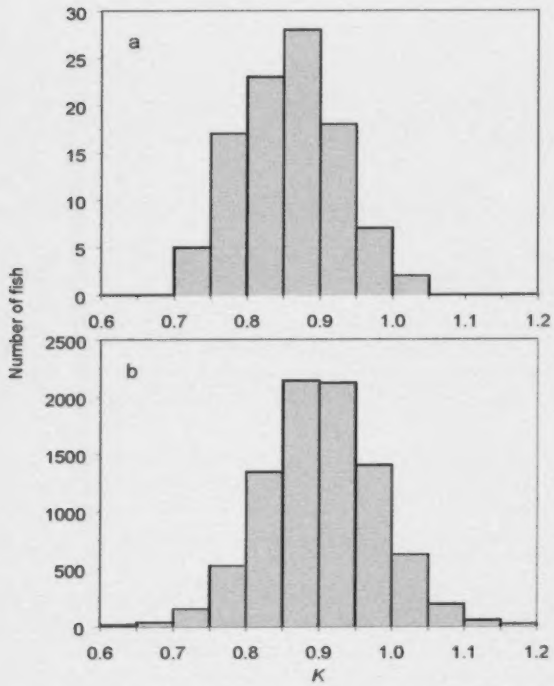

Figure 5. Frequency histograms of Fulton's condition factor (K) for fully mature (stage-5) Scotia-Fundy summer- and autumn-spawning herring collected in (a) September 2001 (n=100, mean=0.857, SD=0.068, median=0.857) and (b) collected over the period 1972-2001 (n=9,175, mean=0.906, SD=0.085, median=0.907).

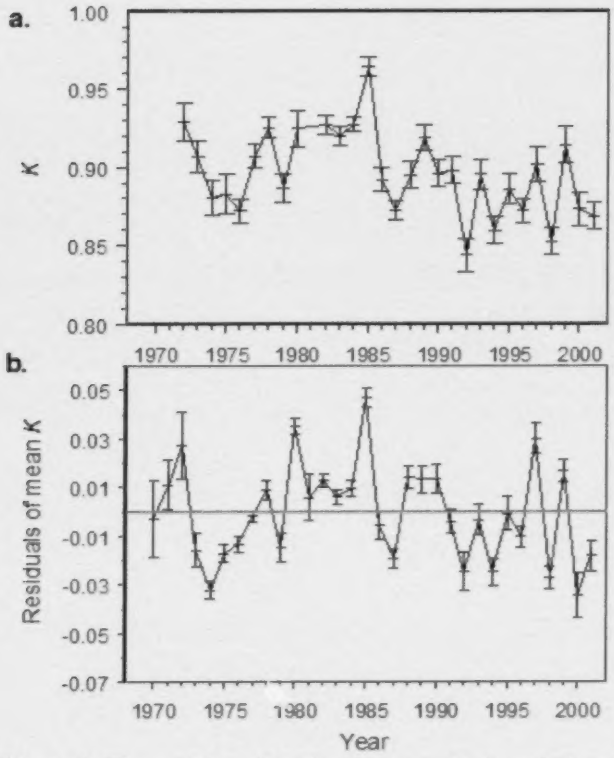

Figure 6. Time series showing inter-annual variation in (a) mean Fulton's K (±2SE) for Scotia-Fundy summer- and autumn-spawning (SFS) herring females at maturity stage-5 during 1972-2001 and (b) residuals around the mean K (±2SE; see eq. 3) for SFS herring females at maturity stage-3 to -5 during 1970-2001).

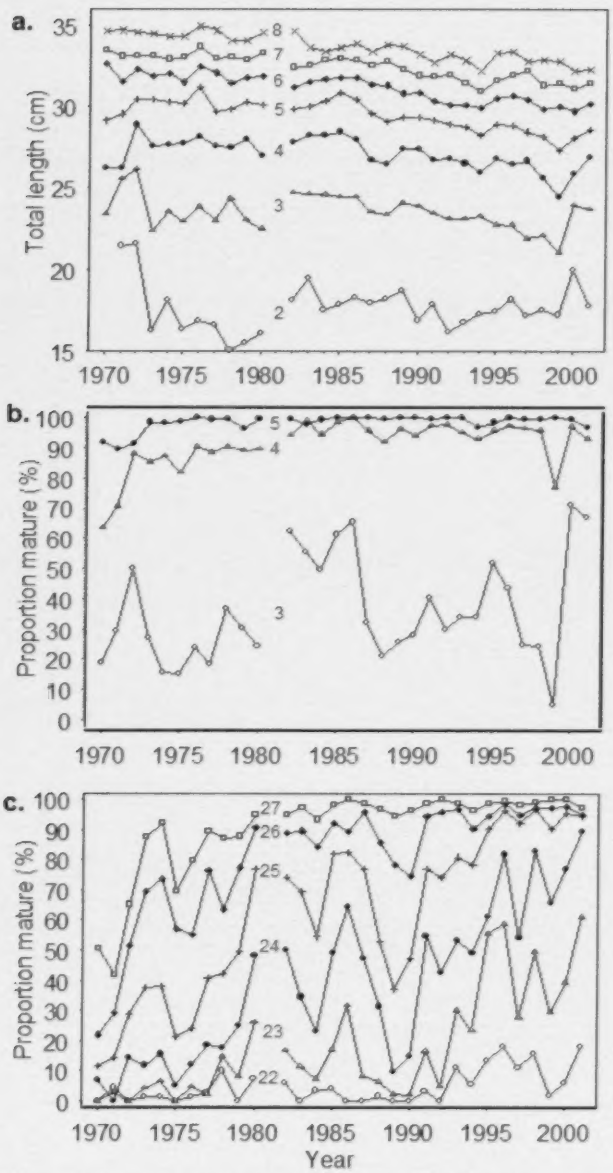

Figure 7. Time series over the period 1970 through 2001 (1981 excluded due to data limitations) for Scotia-Fundy summer- and autumn-spawning herring females collected from sampling in area 4X (Figure 1) of annual estimates of (a) average total lengths (cm) at age–2 through age–8 (noted on graph), (b) the proportion (%) mature among the age–3 to age–5 classes, and (c) the proportion mature among six length classes (22 to 27 cm in 1 cm increments as noted on graph).

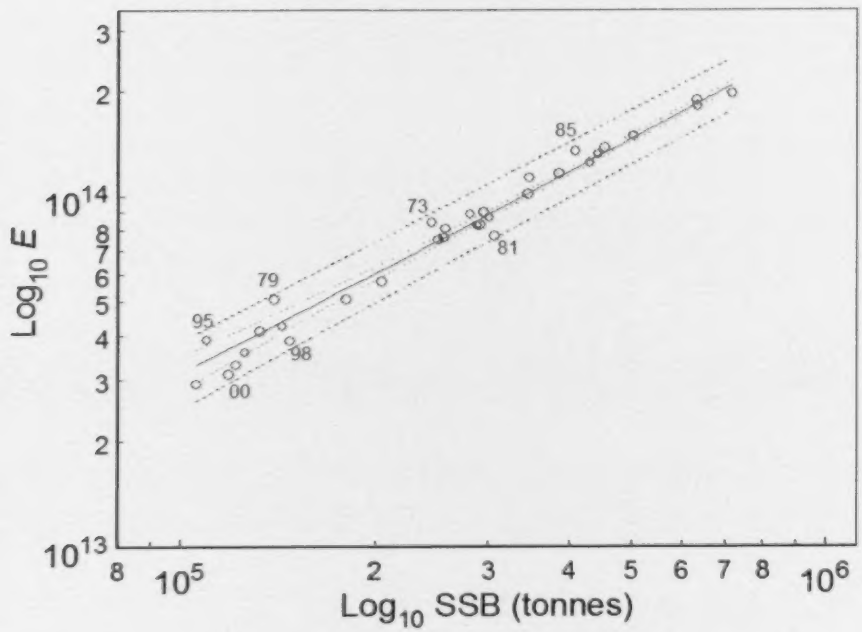

Figure 8. Scattergram of observations (open symbols) and least squares regression (solid line) and 95% confidence interval (dotted lines) around the regression and 95% prediction interval (broken line) showing total egg production (E; $\log_{10}$-scale) as a function of the spawning stock biomass (SSB; $\log_{10}$ tonnes) for Scotia-Fundy summer- and autumn-spawning herring during the years 1970 to 2001 (years referred to in text denoted on the graph). Regression results are provided in text.

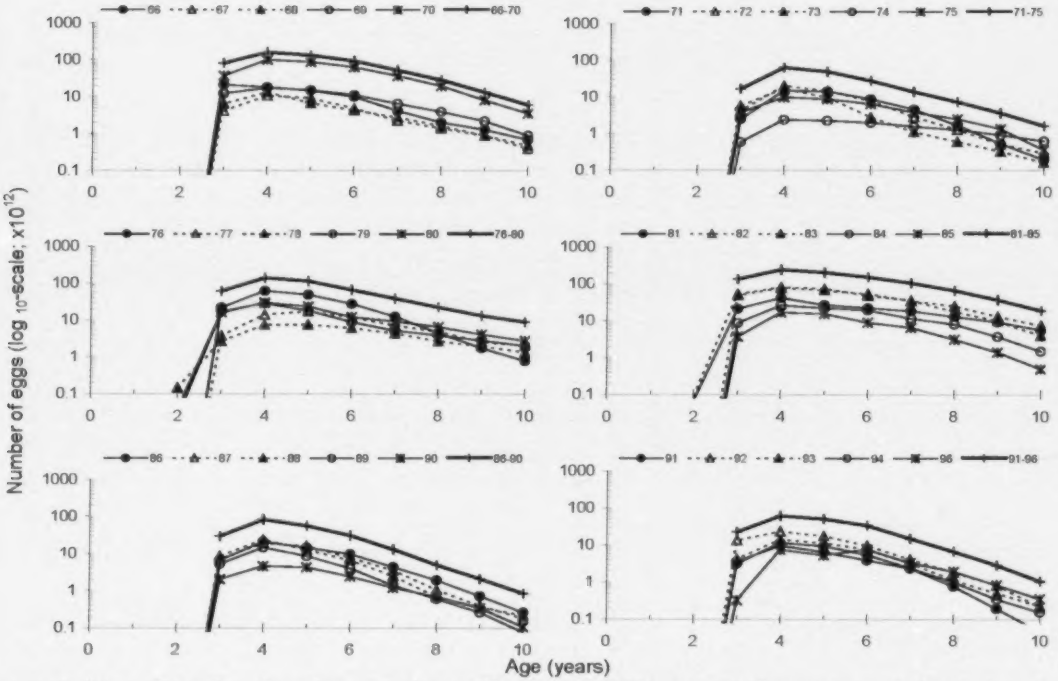

Figure 9. Line plots showing the annual contribution of different age classes (age–2 through age–10) to the total number of eggs estimated to have been spawned by the Scotia-Fundy summer- and autumn-spawning herring (on $\log_{10}$ scale) among year classes from 1966 to 1996 (indicated on the top). Sum over every five year classes shown on each graph is also provided.

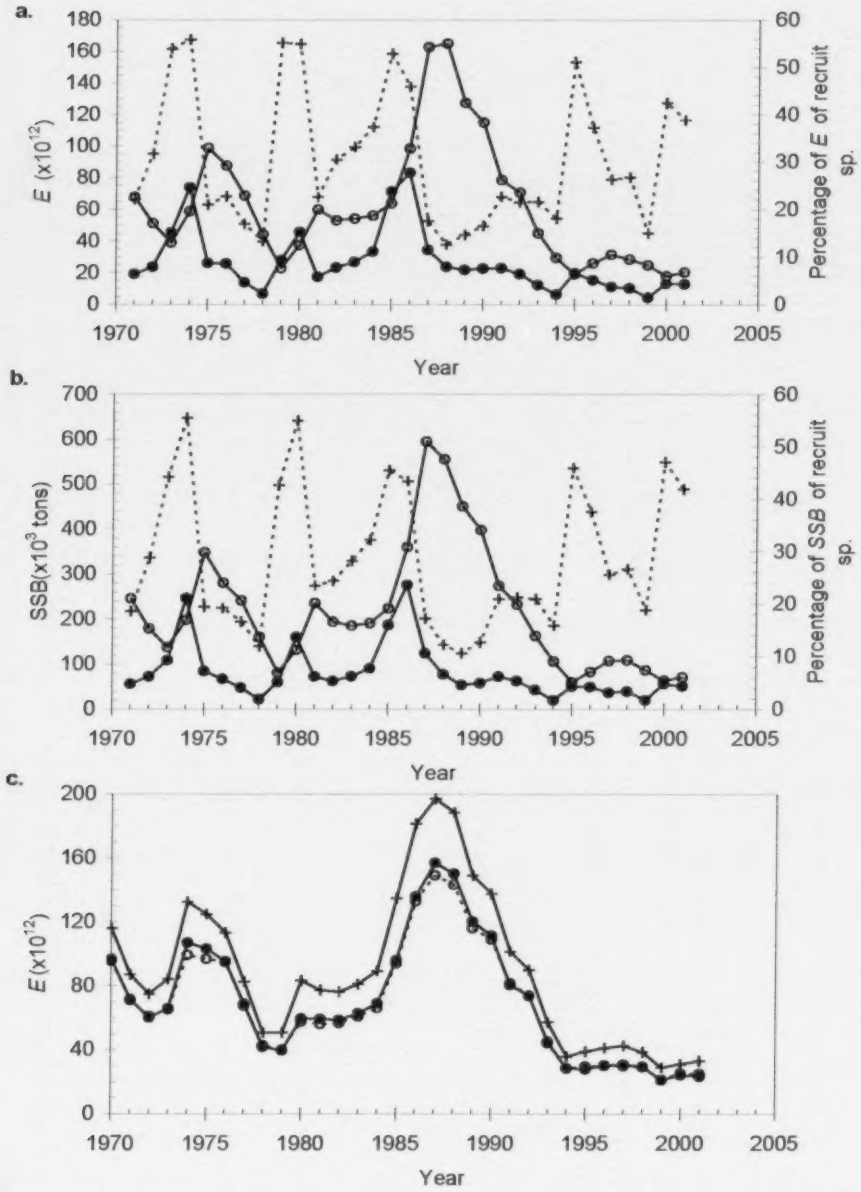

Figure 10. Time series for the Scotia-Fundy summer- and autumn-spawning herring in the years from 1971 to 2001 of (a) annual total egg production (E), (b) annual total spawning stock biomass (SSB) both showing the contribution of recruit- (solid line with filled dots) and repeat-spawners (solid line with open dots), and the annual proportion of E and SSB derived from recruit spawners (in %, dotted line with + on the y-axis to right), and (c) of E estimates derived from our 2001 fecundity analyses using total length and Fulton's K (crosses and solid line), the Perkins and Anthony (1969) relation (solid symbols and line), and the Messieh (1976) relation (open symbols and dotted line) where the latter two fecundity estimates rely on total length only.

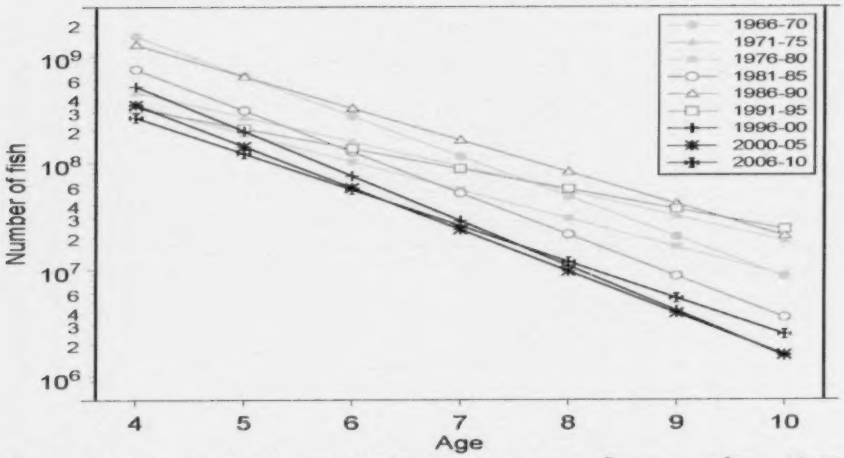

Figure 11. The predicted number-at-age over every five years from 1966-2010 of Scotia-Fundy summer- and autumn-spawning herring from the relationships provided in Table 5.